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FACTS, INTERPRETATIONS, AND EXPLANATIONS: A REVIEW OF EVELYN FOX KELLER'S MAKING SENSE OF LIFE

CRAIG H. KENNEDY
VANDERBILT UNIVERSITY

The job of a researcher is to explain the phenomenon that he or she is seeking to understand. To do this requires the accumulation of facts. These facts are then interpreted to arrive at explanations. However, individual researchers often interpret facts in different ways and arrive at disparate explanations. In her book, *Making Sense of Life*, Evelyn Fox Keller (2002) outlines various approaches used by developmental biologists to understand the animate systems we call life. In this review, I note several parallels between biology and behavior analysis in how facts are discovered, what is an acceptable interpretation of data, and how explanations are arrived at.

DESCRIPTORS: behavior analysis, biology, book review, experimental analysis, explanation, fact, interpretation

> In the settings in which I then worked [theoretical physics], the relation between theory and experimental work was a familiar one. The primary function of experiment was to test theoretical models. . . . Only later, while working as a mathematical biologist and teaching a course to medical students on the uses of mathematical methods in biology, did I get my first glimpse of a more fundamental divide. . . . After introducing a biological problem described in terms of eleven variables, I used dimensional analysis to show that the relations among only three of these variables needed to be studied empirically; all other relations could be inferred logically. The students, however, were clearly unhappy: "But you haven't done the experiments," they complained. "So how can you *know*? How can you be sure?" That question stopped me in my tracks, and I have been thinking about it ever since. (Keller, 2002, pp. viii–ix)

In *Making Sense of Life,* Keller's goal is to understand how researchers explain the phenomena they study. This includes what constitutes elements of an explanation and what elements do not contribute to explanation. In doing so, the book also focuses on how certain assumptions (often implicitly adopted by a research community) influence the types of data that researchers collect and how they interpret that information in pursuit of explanations. Keller avoids explaining explanation in a philosophical sense and, instead, focuses on the functions that various explanations serve for researchers.

To accomplish this goal, Keller surveys the use of explanation in developmental biology during the 20th century. Developmental biology can be described as the study of how organisms come to be. Its focus is on

Keller, E. F. (2002). *Making sense of life: Explaining biological development with models, metaphors, and machines.* Cambridge, MA: Harvard University Press.

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Correspondence should be addressed to Craig H. Kennedy, Department of Special Education, Box 328 – Peabody, Vanderbilt University, Nashville, Tennessee 37203 (e-mail: craig.kennedy@vanderbilt.edu).

the mechanisms of how animals and plants emerge from single cells through cell differentiation and specialization into intact, mature organisms. It is now known that these processes are controlled by cellular and genetic events that occur within individual cells and interactions among cells (Watson, 2003). However, understanding the biological development of organisms has taken a number of twists and turns during the past 100 years on its way to its present status. This sojourn has involved researchers conducting experiments and interpreting their results. Many of these efforts have led to fruitful discoveries that have added to the understanding of plant and animal biology; others have borne lesser fruit or not survived the test of time.

A treatise on explanation in developmental biology should be of interest to behavior analysts for at least four reasons. First, developmental biology has rapidly developed during the last century, moving from notions based in vitalism (biologists' version of mentalism) to the expression of genes to guide the development of organisms (Collins, Green, Guttmacher, & Guyer, 2003). Second, biologists have had to grapple with what constitutes an adequate explanation, including what evidence is included and excluded. Third, because Keller has experience in both theoretical physics and developmental biology, she has a unique perspective on deductive versus inductive, top-down versus bottom-up, and theory-driven versus experiment-driven approaches to explanation. Finally, there are several parallels between how developmental biologists approach their subject matter and how behavior analysts approach theirs.

In this review, I will discuss a selected set of topics from Keller's book. Themes include (a) the role of analogy and structural similarity as bases for explanation and (b) quantitative models versus experimental analyses of biological systems. These areas will be discussed within the context of how they have emerged in developmental biology; but, in addition, I will attempt to draw parallels with similar issues of interest in behavior analysis. First, however, a discussion of some key terms is necessary.

FACTS, INTERPRETATIONS, AND EXPLANATIONS

Keller's book is about explanation, but her exposition of how researchers arrive at explanations is through their conducting research and how they interpret their findings. This approach to explanation is a pragmatic one and fits well with behavior analysts' tendencies toward exploring the function of verbal constructs rather than attempting to structurally define them (Hineline, 1990). Many philosophers of science have discussed, defined, and debated the nature of explanation, only to continue this process without arriving at a definitive meaning for the term (e.g., Knorr-Cetina, 1999; Mulkay, 1991). Breaking with current philosophical approaches to constructivist interpretations of science, Keller adopts an inductive approach: How do scientists use explanation to pursue answers to the questions that interest them? Research is, after all, a systematic approach to answering questions (Sidman, 1960). So what we have, in essence, is a functional analysis (albeit a nonexperimental one) of how researchers arrive at explanations.

Making Sense of Life explores explanations by observing how they are derived from facts via interpretations of data. So, to understand how researchers use explanation, we need to understand what constitutes the facts and interpretations they use to arrive at explanations. To do so, we need to have working definitions of these terms.

Use of the word *fact* will refer to replicable experimental findings that establish some type of functional relation between indepen-

dent and dependent variables (Kennedy, in press). In this sense, a fact is a reproducible experimental result. Each time a researcher does *X* under certain conditions, he or she produces *Y*. If he or she does *X′* under the same conditions, he or she produces *Y′*. Such relations are demonstrable facts. One can argue about what the facts mean, but one cannot deny that they occur and the specific conditions under which they are produced. There are, of course, facts that are not experimentally derived (e.g., I live on Cedar Lane in Nashville, Tennessee, my office is located at the corner of Edgehill and 21st Avenues in the same city, and they are approximately 2 miles apart). However, the focus of Keller's book and, hence, this review, is on experimentally derived knowledge. So, with this caveat, we will refer in this review to repeatable experimental outcomes as facts.

Interpretation is a necessary step between facts and explanations and plays a central role in Keller's discussion of research practices in developmental biology. *Interpretation* will refer to conclusions drawn from facts. That is, given a particular experimental finding, what conclusion does Researcher A draw from the results versus the conclusions arrived at by Researcher B or C. As we will see in the following sections, researchers often accept particular experimental findings as facts, but offer substantively different interpretations of what can be drawn from the facts.

Explanation will refer to verbal statements about how facts and their interpretations are used to identify the controlling variables of a particular phenomenon (Skinner, 1974, p. 156). Explanations are often considered an endpoint for exploring a particular set of functional relations. Once a series of functional relations and interpretations of those relations are offered, an explanation is a statement of causes. To explain something is to understand why it occurs.

The definitions of fact, interpretation, and explanation just offered may be debated for their adequacy, but my interest in their usage is practical. The more pressing issue is that researchers should contemplate these ideas because they influence their comprehension of what they study. Facts may be facts, but as will be illustrated later in this review, different interpretations can be offered for the same facts. Similarly, we will see that not all explanations satisfactorily describe the causes of a phenomenon. Indeed, even those facts, interpretations, and explanations that can withstand critical scrutiny may not endure as a scientific field evolves. These observations beget certain questions that researchers often do not explicitly ask themselves or discuss with others. What is an explanation? How do we know when something has been explained? What results from explaining something? And, how do these issues shape our understanding of a particular subject matter and influence our future experimental activities?

SYNTHETIC BIOLOGY: MORPHOLOGY AS ANALOGY

The goal of biology is to explain what life is (Lamarck, 1809/1984). However, a definitive answer to this question proved to be elusive to researchers in the 19th century. Before biologists began to address this question scientifically, an alternative explanation had been advanced that was accepted by most people: vitalism. When biology emerged as a field, the prevalent belief was that living organisms possess an inner force that gives them the properties of life. It is important to note that this inner force had no physical existence; it was metaphysical.

One of vitalism's strengths was that it explained a wide range of biological phenomena, from why animals were animate to how cells divide. Vitalism was also intuitive; it was easily understood, and it explained

events in the everyday world (Chew & Laubilcher, 2003). This characteristic of vitalism makes it a "rhetorical argument" (Cohen & Nagel, 1962, p. 19). When using rhetoric, an individual is successful when he or she produces an argument that provides the audience with a feeling of certainty, referred to as *unquestionable assurance.* Vitalism provided many people with an assuring and accessible account of animate processes.

Vitalism's greatest strength, however, was that it could not be easily refuted. Because vitalism was a metaphysical explanation, demonstrating it did not exist amounted to proving a negative. Proving that an entity does not exist, when in fact it does not exist, requires a complex logical argument. Proving a negative entails refuting an argument whose claims cannot be proven wrong. This type of argument shifts the burden of proof from the person making the claim (e.g., vitalism is how life works) to individuals who are critical of the claim (e.g., vitalism is a specious explanation).

An example of the complexity of proving a negative is the task of convincingly demonstrating to someone that angels do not exist. The first step should be to show that under all possible conditions no angels can be found. However, the primary problem with proving a negative such as "angels do not exist" is that it is an unprovable statement in that it cannot be exhaustively demonstrated that angels do not exist (e.g., how does one test the proposition, "angels only live in heaven"). Proving a negative primarily rests with the logic that the counterhypothesis to "angels do not exist" has never been demonstrated (i.e., no credible angel sightings have been reported). The argument for rejecting the existence of angels, then, becomes primarily a probabilistic one. Whenever we look for an angel, we never find one (or Martians, Bigfoot, or the Loch Ness Monster). At some point the credibility of the counterhypothesis (i.e., "angels do exist") becomes implausible, and the alternative hypothesis (i.e., "angels do not exist") becomes the only intellectually rational answer.

There is, however, another way of demonstrating that vitalism is an inadequate explanation. If someone could identify the material mechanisms responsible for life, then metaphysical notions such as vitalism would be superfluous. Such a strategy is often referred to as *mechanism, materialism,* or *reductionism* by philosophers of science, because they are based on the interaction of material events that provide a causal explanation for the larger system. An early advocate of discovering alternatives to vitalism was Jacque Loeb (1912/1964), a physicist and biologist who had a major influence on such notable 20th century scientists as William Crozier and B. F. Skinner (Bjork, 1993; Boakes, 1984).

A primary means, advocated by Loeb, for discovering a mechanistic explanation for living organisms was the production of life from artificial matter. If a researcher could produce a living organism from inorganic materials, then a metaphysical force was unnecessary to create life. All that was required were the necessary ingredients in the form of certain molecules being combined under certain conditions.

Artificial Organisms

Several biologists in the early 20th century took up this challenge to refute vitalism and find an explanation for how living organisms develop. The most notable of these was Stéphane Leduc (1912), a French biologist who focused his career on creating what he referred to as *artificial organisms*. This approach has since become known as synthetic biology, with the term *synthetic* referring to the combining of chemical elements to produce a distinctly different substance. The goal of synthetic biology was to identify the physical mechanisms that gave rise to life.

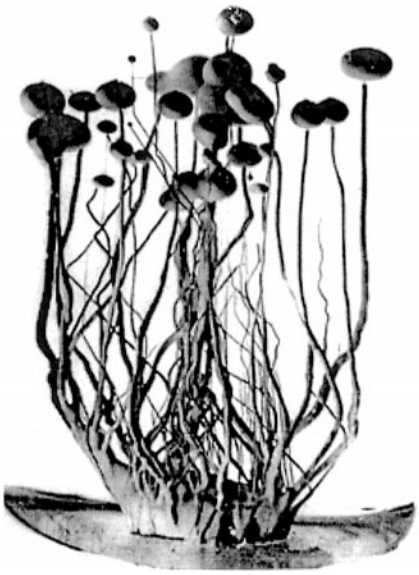

Figure 1. Reprint of one of Leduc's morphological forms (Leduc, 1912, Figure 40).

What Leduc (1912) did was combine several readily available chemicals in a fluid medium and observe what emerged. The results were astounding. By combining calcium and nitrate in a solution of sodium silicate, Leduc could produce growths closely resembling fungi (see Figure 1). By altering the types of chemicals used, he could produce osmotic growths resembling not just fungi, but a variety of plants (e.g., ferns) and sea animals (e.g., sea-urchins). These osmotic growths not only resembled living organisms, but they grew over time and appeared to produce new growths akin to reproduction. Adding to the impressiveness of Leduc's discovery, not only was he able to replicate entire organisms, but he could also produce results that mimicked intracellular processes. For example, Leduc could simulate some of the physical features involved in cell division (e.g., mitosis). As a collection, these findings provided a compelling case that osmotic growths could be produced and resembled a range of biological phenomena.

There is no doubt that what Leduc (1912) created was real, in the sense that his osmotic growths could be replicated in other laboratories by other researchers (i.e., his findings were facts). What he produced was not quackery. What is at issue, however, is how he interpreted these data. For Leduc, morphological analogy was sufficient to claim that he had produced artificial life. Because the osmotic forms looked (and in some cases acted) like living organisms, in Leduc's view he had found the conditions necessary to create organic life.

This interpretation of the data led to an important logical error on the part of Leduc (1912). Although many of his contemporaries agreed that he had created physical structures that resembled organic life, they viewed the interesting forms as imitations. Critics noted that osmotic growths were no more living animals than marble statues of people were humans (e.g., Macfarlane, 1918). Although Leduc produced physical structures that morphologically resembled animate life (in form and action), the structures themselves were not alive and could not produce living organisms. That is, they were only physical analogies.

Leduc (1912), however, took his observations a step further. He noted that he had identified the necessary material components to produce life, thus providing an alternative to vitalist theories and establishing the basis for how life is created. As quoted by Keller, Leduc noted,

> When we see under our own eyes the cells of calcium become organized, develop and grow in close imitation of the forms of life, we cannot doubt that such a transformation has often occurred in the past history of our planet, and the conviction becomes irresistible that osmosis has played a predominant role in the history of earth and its inhabitants. (Keller, p. 28)

These conclusions about his data led Leduc (1912) to confuse producing artificial

life and artificially producing life. The former creates "organisms" that physically resemble plants and animals; the latter creates living organisms from physical materials. In this instance, the overinterpretation of data led Leduc to an explanation of the basis for life that was untenable. Although Leduc's work received a great deal of attention in the early 20th century, within a few decades reference to his work stopped. Therefore, a definitive refutation of vitalism would have to wait until the emergence of molecular biology (discussed later in this review).

Cellular Automata

Lest the reader think such issues are only historical, Keller points out that contemporary research in evolutionary biology may parallel some of the interpretative issues raised by synthetic biology. In particular, work on computer simulations of biological phenomena, often referred to as *cellular automata,* may be testing the limits of morphological analogy (Wolfram, 2002). Using cellular automata, researchers can simulate biological dynamics in an attempt to better understand how animate systems work at the cellular or organismic level. Thus, at the cellular level, cellular automata are not the living cells comprising living tissue; they are simulated cells of simulated tissue. In this regard they are not unlike simulations of neural networks that do not involve actual neurons and glia but are computer simulations of interactions among simulated brain cells. The use of computer simulations, according to Keller, emerged in the 1980s in the physical sciences as a means of modeling complex systems (such as thermonuclear processes) and is viewed as a productive approach to understanding such phenomena.

Building on the success of simulations in other areas, some researchers, most visibly Langton (1997), have offered a similar approach to understanding biological systems. Using the concept of cellular automata, researchers have attempted to study complex biological processes such as species differentiation within a population. As used by Langton, cellular automata refer not to individual cells that comprise some type of tissue or organ but to individual organisms that can be defined to act or react in specific ways via computer software. That is, a cellular automaton represents an individual member of a species. Therefore, a cellular automaton may be defined as an individual animal from a species that has a genotype (i.e., its individual genetic makeup) that is expressed as a specific phenotype (i.e., physiological and behavioral characteristics). A simulation then proceeds across time in which individual automata produce offspring that have varied genotypes that lead to differentiation among phenotypes, potentially altering the probability of successful reproduction by an individual unit (i.e., passing on its genotype to the successive generation of automata). By conducting such simulations, researchers have attempted to study evolutionary processes that are not accessible from fossil records or real-time observations (see Schellnhuber, 1999).

Using such simulations, researchers can vary parameters such as survival and reproduction probabilities to analyze possible evolutionary processes. Interestingly, many researchers in this area have taken an interpretive step beyond their data that might be viewed as similar to that of Leduc's (1912) work on synthetic biology. Simulations of evolutionary processes are algorithms written into computer programs. However, some researchers have taken this process and added a layer of interpretation that parallels evolutionary biology. For example, Ray (1998) uses terms such as *genes, genetic crossover, energy,* and *reproduction* to refer to specific variables in a simulation algorithm. This approach is referred to as *A-Life,* alluding to artificial life. An example might be describing the formula X plus Y divided by Z as

organismic energy (X) plus reproductive fitness (Y) divided by food availability (Z). When researchers who use these simulations discuss their work, they use biological terms to describe not only their results but also the variables that contribute to their findings.

This interpretation of data is similar to synthetic biology (see previous section on *Artificial Organisms*) in that researchers are imposing a judgment about the meaningfulness of their findings that is beyond the actual facts. However, in the use of cellular automata in evolutionary biology, morphological analogy is primarily linguistic rather than visual (Hayles, 1996). By describing discrete variables from a computer algorithm using terms from evolutionary biology, such research imparts on itself a level of legitimacy that is interpretative, not factual. Such linguistic practices have the enticing sound of being actual analyses of evolutionary processes, but the character strings of the algorithm could just as well be interpreted as characterizing a hurricane system or a nuclear reaction. Whether the practices of researchers of A-Life depart from synthetic biology, in that it becomes scientifically productive, awaits to be seen (Bernstein, 2003).

Behavior-Analytic Analogues

A major theme in Keller's book is that all researchers make interpretations regarding their findings. One cannot attempt to solve meaningful problems without interpreting findings to arrive at explanations. The issue for Keller is when are such interpretations scientifically productive. At this point it might be useful to discuss morphological analogy in the context of behavior–environment relations studied by behavior analysts. I will offer two examples: facilitated communication and animal models.

The finding that people with autism can type elaborate verbal statements and answer complex questions when another person without intellectual disabilities physically supports their fingers and hands is not controversial. This outcome has been replicated enough times that a reasonable person would accept it as fact. What is highly controversial is how this fact is interpreted to arrive at an explanation of the phenomenon.

One perspective, advanced by advocates of facilitated communication, suggests that the communication arises from the person with autism and is due to a profound apraxia that is overcome by the assistance of another person (Biklen, 1990). An alternative perspective suggests that the communications that arise from this technique are from the individual who provides the assistance, not the person with autism (Green & Shane, 1994). Both of these interpretations arise from the same data but draw profoundly different conclusions about the nature of events being explained.

The former perspective is based on the observation that the individual with autism, not the person facilitating his actions, generates the behavior. In essence, supporters of this interpretation of the data are basing their conclusions on the morphology of what is produced (e.g., written words), similar to the morphological analogies drawn by researchers in synthetic biology. The latter perspective is based on additional experimental evidence that controls for possible influences from the people involved in producing the communication. This experimental approach suggests that the facilitator is the source of the communication.

It should be noted that biology is largely an empirical discipline, much like behavior analysis. Biologists and behavior analysts are taught to trust their data because they are based on experimental analyses of what is trying to be understood. The procedures and methods used to generate these data require intense scrutiny, but what results from experimentation is considered veridical. From this perspective, the discrepancies in interpretation between ethnographers (e.g., Bik-

len, 1990) and behavior analysts (e.g., Green & Shane, 1994) may be based on how people in various disciplines are taught to interpret data and draw conclusions to explain what they are trying to understand.

Another example of morphological analogy that has become a foundation of biomedical research is the use of animal models. Animal models use analogue situations for a problem and analyze the model to reveal processes that might improve human health and behavior. This logic is not new to behavior analysis. In the mid-20th century, Skinner conducted a series of experiments that modeled issues relevant to people in their everyday lives using pigeons and rats as subjects.

One example relevant to human behavior that Estes and Skinner (1941) analyzed was anxiety. Rats were taught to press a lever on an intermittent schedule of food reinforcement that produced a continuous, moderate rate of responding. Over this baseline a signaled positive punishment contingency was established. At various intervals a tone sounded, followed a few minutes later by an inescapable shock. After the shock was delivered, the tone was terminated. Throughout this process, the intermittent schedule of food reinforcement was operative.

The experimental results demonstrated that rats would press the lever for food in a pattern typical of intermittent reinforcement schedules, but as soon as the tone started, responding ceased. As soon as the shock occurred and the tone stopped, the animal resumed its lever pressing for food reinforcement. There was no reason for the rat to stop lever pressing when the tone began, but the tone was associated with a noxious stimulus that suppressed other, more functionally relevant, operants. This effect on behavior was interpreted by Estes and Skinner (1941) as being related to human behaviors that society tends to label as anxiety.

Behavior analysts may not view these experimental extrapolations to human behavior as terribly contentious, but that is because of the training they receive. Behavior analysts are taught that laboratory analogues of human situations are a viable, and often necessary, approach to understanding human behavior. Similar strategies are routinely used by biologists, for example, by studying *Drosophila* to understand sleep regulation (e.g., Shaw, Cirelli, Greenspan, & Tononi, 2000). Others have not been so sanguine about animal models. Skinner, during his life, was often attacked by critics, not for his experiments, but because of his interpretation of his experimental findings. Skinner used his laboratory findings to explain why people gambled, made love, or fought (e.g., 1953). Many people, both laypersons and scientists, found such extrapolations to be inappropriate and troubling (Smith & Woodward, 1996).

To take morphological analogy one step further, consider the case of animal models that look for functional similarities in humans and nonhumans in often disparate topographies of behavior. A good example of this is the Porsolt swim test as an animal model of human depression (Porsolt, 1979). The Porsolt swim test uses animals, such as mice, that are placed in water and their swimming is observed. A primary dependent variable in this test is the length of time the animal swims before it stops. In general, the longer the animal swims the less depressed it is considered to be. On the surface this sounds implausible and even a little silly. However, when psychotropic drugs that are known to improve depression in people are administered in these tests, the animals swim longer. In fact, many drugs used to treat depression (e.g., selective serotonin reuptake inhibitors like fluoxetine) were initially screened using tests like the Porsolt swim test. It has also been useful in identifying the subtypes of serotonin receptors involved in the drug action of antidepressants (Skolnick,

1999). Whether animals that stop swimming are depressed is secondary to the fact that it is a productive experimental model of human depression.

My point in these various examples has been to demonstrate how relative the appropriateness of morphological analogy is. Like most concepts in research, the viability of morphological analogy depends on how it is used in a particular experimental context. Leduc's (1912) overinterpretation of his data in an effort to refute vitalism and arrive at a materialist explanation of biological development was a failure. Computer simulations of A-Life may, or may not, become productive scientific strategies. Facilitated communication has proven to be something very different from what was originally claimed. Animal models of human behavior have a long track record of success, despite sometimes being counterintuitive. All of these examples have used morphological analogy in one way or another to interpret data and arrive at an explanation for a particular phenomenon, with varying degrees of success.

MATHEMATICAL BIOLOGY: QUANTITATIVE MODELING VERSUS EXPERIMENTAL ANALYSIS

The search for an alternative to vitalism took a new direction in the mid-20th century. Rather than focusing on creating life from inanimate materials, researchers focused on the molecular building blocks of life (Watson, 2003). The key event in this research was the discovery of the structure of deoxyribose nucleic acid (DNA) by Watson and Crick (1953). This discovery shifted the focus of biologists toward the study of DNA and away from how to create life. This marked a fundamental shift in how biologists conceptualized the problems they were attempting to solve.

The question biologists began to focus on was how sequences of DNA regulated the activity of individual cells. This focus was simultaneously cellular and genetic. It was cellular in that researchers began focusing on how cells developed, formed into certain structures (e.g., the central nervous system), and regulated their activity through intra- and extracellular processes. It was genetic in that the composition of chromosomes in terms of DNA sequences were the molecular mechanisms that determine cellular processes. The expression of certain genes within the nucleus was the regulatory mechanism for cells and life.

We now know that biologists interested in how cells develop to form living organisms need to understand how gene expression regulates cell division, migration, specialization, and homeostasis (de Villis & Carpenter, 1999). However, prior to the discovery of DNA, biologists were already interested in understanding development in ways that departed substantially from approaches such as synthetic biology. One such approach was the mathematical modeling of biological processes that emerged in the 1930s.

Mathematical Explanations

In Keller's history of developmental biology, she identifies Rashevsky (1934) as the key person in the establishment of what was then referred to as *mathematical biophysics* and now is referred to as *mathematical biology.* Rashevsky's goal was to establish a theoretical approach to biology that was similar to theoretical physics. Rachevsky was a physicist by training and, hence, was very familiar with using quantitative methods to model and explain phenomena. Before becoming interested in biology, he focused on the onset of instability in liquid droplets.

For theoretical physicists, much of what constitutes explanation is derived from the ability to quantitatively model a particular phenomenon. If the equation adequately describes certain events, then a formal explanation of the phenomenon has been

achieved. Accordingly, Keller notes, "causal responsibility is assigned not to particular material entities or events but rather to a set of interaction dynamics" (pp. 101–102). An example of this approach to explanation in mathematical biology is Turing's (1952) development of a mathematical solution to morphogenesis.

The question Turing (1952) was interested in was how cells interact to form structures (e.g., embryogenesis or the spots on a leopard). To do this, he identified an idealized theoretical system that contained the minimum number of variables necessary to produce morphogenic patterns. The details of the resulting differential equations are not important in this context, but their role in arriving at an explanation is. Turing's mathematical solution to morphogenesis used an equation that could be used to produce shapes similar to cell assemblages observed in nature. For Turing, this mathematical model explained morphogenesis. As Keller notes, in "Turing's effort, we are presented with a veritable caricature of the mathematical physicist" (p. 95).

Explanatory Satisfaction

The question is, "Is this an adequate explanation?" The answer to that question depends on what criteria one uses to judge a scientific explanation as adequate. To a mathematical biologist or theoretical physicist, Turing's (1952) solution is eloquent and robust. To an experimental biologist, Turing's solution is an idealization that may or may not exist as a fact. Which of these the reader believes is preferable depends on his or her own learning history.

Although biologists study a range of phenomena and use a variety of methods, one thing is clear: They learn about their area of interest through experimentation. Ask a biologist what he or she does and he or she will very likely describe the experiments the research team is conducting. As the introductory quote in this review suggests, most people interested in biology are predisposed by training and experience to conduct experiments to understand biological phenomena.

A researcher can develop an eloquent hypothesis about how a biological process functions, but it is only his or her best guess about how nature works. To paraphrase a statement attributed to the astronomer Sidney van den Bergh about hypotheses and experimentation, "Our job is to listen to what nature is telling us and not impose our own aesthetics." A researcher's prediction regarding the outcome of an experiment may be correct, partially correct, or simply wrong. However, for an experimentalist, the primary means of finding out the viability of a hypothesis, and far more important, the actual results, is by conducting an experimental analysis. As noted by Keller,

> Can, for example, mere arm-chair theorizing—work that requires only paper and pencil and not the manual labor of actual experiment—serve as an adequate basis for epistemological entitlement? The judgment of most experimental biologists of the past century (and especially of those working in the United States) has been a decisive no. (p. 77)

This bias toward experimentation among biologists, as well as behavior analysts, is primarily an issue of what constitutes a fact. Where do facts come from? Can someone just state an assertion and consider it a fact? In some areas of science, particularly theoretical physics, the answer to this latter question is a qualified yes. However, in the history of biology, facts are derived from experiments, not from armchair analysis. Experimental facts represent how nature works. Whether we could have predicted the results, or even whether we adequately understand them, is an issue of lesser importance.

Table 1
E. B. Wilson's (1934) "Axioms and Platitudes" Regarding Mathematical Biology

1. Science need not be mathematical.
2. Simply because a subject is mathematical it need not therefore be scientific.
3. Empirical curve fitting may be without other than classificatory significance.
4. Growth of an individual should not be confused with the growth of an aggregate (or average) of individuals.
5. Different aspects of the individual, or of the average, may have different types of growth curves.

This disposition toward gathering facts through experimentation has made biologists resistant to approaches based on mathematical modeling.

This bias toward experimentation was very evident in the reception that Rachevsky's work received from biologists of his day. When Rachevsky (1934) presented his ideas at the Cold Spring Harbor Symposia for Quantitative Biology, one of his fellow speakers (Wilson, 1934) commented on the limitations of mathematical modeling in biology. Table 1 shows a summary of Wilson's concerns about the ability of mathematical modeling to render meaningful conclusions about biological phenomena. The first concern is that quantitative models describe existing structures but do not explain how they come into existence; hence, Statements 1 through 3 in Table 1 regarding the relation between science and math. Wilson's second area of concern had to do with population genetics and the description of individual elements by group averages (Table 1, Statements 4 and 5) (see also Sidman, 1952). Wilson viewed Rachevsky's efforts as too remote from what he was trying to explain.

For Wilson (1934), biology was an inductive, empirical discipline, not a deductive, theory-driven endeavor. Keller describes this lack of affinity among experimental biologists for mathematical modeling by using the concept of *explanatory satisfaction*. An "explanation is . . . to provide a causal account of a phenomenon . . . the expectation of a causal account is that it will identify the agent or event responsible for the effect" (p. 101). For a theoretical physicist, explanations can be analogical. That is, mathematical models can be used to describe the necessary conditions for an effect via equations, even though no demonstration using naturally occurring events has occurred. According to Keller, however, this type of explanation is unsatisfactory for experimental biologists because they have been trained to analyze natural systems, not idealized systems. "For those who expect an explanation to identify particular causal loci, such an account [i.e., mathematical modeling] is *a priori* unsatisfactory" (p. 102).

Experimental biologists in the era of molecular biology seek explanations for cellular processes at the genetic level. There is physicality to what causes something and a mechanism that is identified in explanations produced by experimental biologists. For example, a particular gene in the genome of an animal (e.g., the *tlx* gene), when expressed, is the mechanism that guides neuronal cell migration in a particular area of the brain (i.e., the limbic system) (see Monaghan et al., 1997). In this example, there is a specific physical event that occurs at the molecular level that causes particular events to occur at the cellular level, or in their absence, not to occur. From Keller's perspective, these types of events characterize causal explanations for developmental biologists (p. 102).

However, it is interesting that more mature sciences, such as physics, will admit information into their explanations (i.e., quantitative models) that many biologists view with skepticism. Could it be that biology is not yet ready for such an approach or is its purview not amenable to mathematical modeling? Keller concludes that experimental biology will eventually view mathematical

modeling as a desirable approach to understanding animate life, but that there will need to be clear benefits to experimentalists for admitting such data into their explanations (p. 112).

Behavior-Analytic Analogues

Behavior analysts have not yet focused on a top-down approach to modeling behavior processes, preferring instead to construct explanations from experimentation. However, even though most behavior analysts' focus is on direct experimentation, some individuals have suggested that modeling may have a place in this discipline. Early in Skinner's career (1938), he focused on a model to explain response probability in relation to reinforcement referred to as the *reflex reserve*. Although not a mathematical model, the reflex reserve used mechanical metaphor to describe how response probability changed in relation to reinforcement (Killeen, 1988). Skinner abandoned the use of the reflex reserve in favor of describing functional relations, finding modeling not as useful as experimental analysis (Skinner, 1979). In this case, he found the accumulation of data in a new area of research to be more productive than the development of an explanatory system.

More recently, Killeen (1992, 1995) has attempted to treat behavior–environment relations from a perspective consistent with theoretical physics. In this work, Killeen has used quantitative modeling to predict and describe behavioral functions that have yet to be established in the laboratory (e.g., components of response strength). This approach uses mathematical models to develop idealized systems that are integrative of current findings and predictive of new functional relations. Whether this approach to making a priori predictions about behavioral processes is productive remains to be seen.

Researchers in the experimental analysis of behavior have been using quantitative modeling since the 1970s to integrate experimental findings and arrive at parsimonious descriptions of existing data. This work has been most active in the areas of choice and behavioral momentum (see Fisher & Mazur, 1997; Nevin & Mace, 1994). Unlike mathematical biologists, quantitative modelers in these areas have looked to develop equations that can be fit to extant data. This differs substantially from the process used by Rachevsky (1934) and Turing (1952), who sought to model first and let others test the adequacy of their theories.

An issue that has emerged from quantitative modeling in the experimental analysis of behavior is the relative adequacy of molar versus molecular accounts of behavior–environment relations (Baum, 2002). The issue is at what level behavioral data are most productively interpreted—in large aggregates or smaller units. In molar accounts of behavioral events, the goal is to characterize them in averages of aggregate events over extended periods of time. In molecular accounts, the focus is on moment-to-moment contingencies between stimuli and responses. An example of how these different approaches can be used to arrive at divergent explanations of the same set of events is the analysis of why variable-ratio (VR) reinforcement schedules occasion higher response rates than variable-interval (VI) reinforcement schedules do.

VR schedules produce higher rates of responding than VI schedules, but this difference cannot be accounted for by reinforcement rate alone because different response rates can be generated even when reinforcement rate is held constant (Catania, Matthews, Silverman, & Yohalem, 1977). Molecular accounts of this phenomenon have focused on moment-to-moment relations. For example, interresponse time (IRT) reinforcement theory (Shimp, 1968) suggests that the lower response rates on VI schedules are due to the reinforcement of longer IRTs

on these schedules relative to VR schedules, on which brief IRTs are more likely to be reinforced. Molar accounts, such as response–reinforcer correlation theory, have focused on the relation between average response rate and overall reinforcement rate, with VR schedules generating a linear relation between reinforcement rates and response rates.

Either approach to explaining this behavioral phenomenon appears to be adequate, but the explanations are arrived at by taking into account different processes at different analytical levels. Molar accounts tend to summarize large aggregates of behavior–environment interactions to arrive at conclusions about data, whereas molecular accounts tend to use discrete contingency events as the focus of analysis. Behavior analysts who focus on molar accounts of behavior tend to use quantitative models to describe and explain behavioral phenomena, whereas molecular accounts often use visual displays of data as an analytical approach. As noted by Hineline (2001), both accounts have certain benefits and may be viewed as explanations for the same phenomena that occur at different levels of scale. Which is the preferable explanation may depend on the particular question being posed.

Keller notes that with the advent of molecular biology and a focus on DNA as the underlying mechanism in developmental biology, there may be a renewed interest in mathematical biology as an adjunct to experimental biology (p. 108). For example, after the regulatory genes involved in embryogenesis have been identified and their mechanisms explained, there may still be a role for mathematical models (e.g., Turing, 1952) in explaining how multicellular structures develop into certain forms. Perhaps the issue is whether experimental biologists will ultimately find mathematical models useful in arriving at explanations of actual biological events rather than abstracted systems. Behavior analysis may, or may not, follow a similar path.

CONCLUSION

A number of authors have noted that behavior analysis has its historical roots in biology (Boakes, 1984; Schneider, 2003; Thompson, 1984). As this review has attempted to show, although contemporary behavior analysis and biology have little contact with each other, there are strong similarities in how these disciplines approach their respective subject matter. Whether this approach is required to study animate life or is part of the process of nascent disciplines building a systematic and replicable basis for future growth remains to be seen. What is clear is that behavior analysts are not alone in their preference for experimental analysis over armchair theorizing.

> As scientists in the modern era, we generally proceed under the assumption that phenomena, if they are natural, are ipso facto explicable—obliged, as it were to make sense to us. . . . But by what mandate is the world obliged to make sense to us? Is such an assumption even plausible? I would say no, and on a priori grounds. One need invoke neither divine intervention nor unknown forces. . . . The human mind does not encompass the world; rather, it is itself a part of that world, and no amount of self-reflection provides escape from that limitation. (p. 295)

Perhaps, when faced with complex biological systems at the start of a new scientific discipline, the best one can do is experiment and find out how systems are structured and function. This strategy worked well for biologists who began their research a century before Pavlov, Thorndike, and Skinner. Forgoing the development of a priori systems and the overinterpretation of findings may,

in the short term, seem intellectually conservative, but in the long run may be the most efficient process for arriving at adequate explanations of biological phenomena, including human behavior. To paraphrase a quote from Skinner that often appears in the back pages of the *Journal of the Experimental Analysis of Behavior,* "Regard no practice as immutable. Change and be ready to change again. Accept no eternal verity. Experiment."

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